Sex-Biased Phoretic Mite Load on Two Seaweed Flies: *Coelopa frigida* and *Coelopa pilipes*

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Environ. Entomol. 38(6): 1608–1612 (2009)

ABSTRACT Two hypotheses explain male-biased parasitism. Physiological costs of male sexually selected characteristics can reduce immunocompetence. Alternatively, ecological differences could generate male-biased parasitism. One method of comparing the importance of the two theories is to investigate patterns of phoresy, which are only likely to be generated by ecological rather than immunological differences between the sexes. Here we studied the pattern of phoresy of the mite, *Thinoseius fucicola*, on two species of seaweed fly hosts, *Coelopa frigida* and *Coelopa pilipes*. We found a highly male-biased pattern of phoresy of *T. fucicola* on both species. These are the first reported instances of sex-biased phoresy in a solely phoretic parasite. We also show the first two cases of size-biased phoresy. We suggest that ecological factors, particularly, male mate searching, generated male biased patterns of phoresy. We highlight the potential importance of studies of phoresy in determining the relative roles of the immunocompetence and ecological theories in generating male-biased parasitism. We suggest that more studies of patterns of phoresy are carried out to allow detailed comparisons with patterns of parasitism.

KEY WORDS sex-biased parasitism, coelopidae

Sex biases in parasitism have been reported in a wide range of vertebrate taxa including mammals (Poulin 1996, Schalk and Forbes 1997, Moore and Wilson 2002), birds (McCurdy et al. 1998), fish (Reimchem and Nosil 2001), and amphibians (Tinsley 1989). Two main hypotheses have been proposed to explain why males should be more infected (Folstad et al. 1989, Zuk and McKean 1996). Physiological differences, such as reduced immunocompetence in males as a result of higher costs of producing sexually selected traits, can generate higher levels of infection in males (Folstad et al. 1989, Folstad and Karter 1992, Kurtz and Sauer 1999). Testosterone has been found to have an immunosuppressive effect in males, reducing their ability to fight off infections (McCurdy et al. 1998). Testosterone is thought to be particularly important in generating male-biased parasitism across vertebrate taxa (Alexander and Stimson 1988, Folstad et al. 1989, Poulin 1996, Zuk and McKean 1996, McCurdy et al. 1998, Moore and Wilson 2002). Male-biased parasitism in mammals is also associated with increased male-biased sexual size dimorphism (Moore and Wilson 2002), although a similar pattern does not seem to be present in birds (McCurdy et al. 1998).

Far fewer studies have been carried out on invertebrate hosts. Some of these have shown a bias toward higher levels of infection in male hosts (Wedekind and Jakobsen 1998). However, a meta-analysis of all invertebrate data showed no evidence of a consistent bias in the sex of the host (Sheridan et al. 2000). Since the publication of this review, a few other studies have been conducted. One showed a male bias in infections of two dragonfly species by the same mite (Lajeunesse et al. 2004), whereas others showed female biased infections of a beetle (Seeman and Nahrung 2004) and a damselfly (Robb and Forbes 2006). Although invertebrates lack sex-specific steroid hormones such as testosterone, physiological differences between the sexes as a result of variation in the costs of reproduction could still generate male-biased parasitism. Sexual selection is just as likely to act more strongly on male invertebrates as male vertebrates generating higher costs of reproduction (Clutton-Brock and Parker 1992, Owens and Thompson 1994). Unequal costs of reproduction associated with the production of sexually selected ornaments can still affect levels of immunity in the absence of testosterone. For example, reduced male immunities have been reported in a scorpion fly (Kurtz and Sauer 1999) and are believed to play a role in male biased parasitism in a copepod (Wedekind and Jakobsen 1998).

Ecological differences can also generate male-biased parasitism in both vertebrates and invertebrates. For example, behavioral differences might result in males having higher exposure levels than females, as seen in dragonflies (Lajeunesse et al. 2004). While searching for mates, males may encounter a higher number of other individuals increasing the chances of

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parasite transmission. Males can also pick up more parasites by simply traveling between females (Seeman and Nahrung 2004). Additionally differences in the diet of the two sexes might also vary their exposure to parasites (Reimchem and Nosil 2001).

The relative importance of the physiological and ecological models of male-biased parasitism has been the subject of debate (Zuk and McKean 1996, Reimchem and Nosil 2001). In vertebrates, testosterone is generally believed to be the most important factor (Folstad et al. 1989, Poulin 1996, Zuk and McKean 1996, McCurdy et al. 1998, Moore and Wilson 2002). The fact that invertebrates lack testosterone and a consistent male bias in infection (Sheridan et al. 2000) adds support to the testosterone-driven immunocompetence hypothesis as the main explanation of male-biased parasitism in vertebrates. However, some authors (Zuk and McKean 1996, Reimchem and Nosil 2001) have criticized the fact that most studies reporting sex-biased parasitism did not attempt to identify any underlying ecological cause. Consequently, the importance of ecological variation between the sexes is likely to have been underestimated. Ecological causes of sex-biased parasitism such as variation in diet and sexual dimorphisms that have evolved through natural (as opposed to sexual) selection could also play a significant role in generating sex-biased parasitism (Reimchem and Nosil 2001). Furthermore, associations between level of parasitism and exaggeration in a sexually selected trait could have an ecological explanation.

A recent study (Lajeunesse et al. 2004) suggested that phoretic associations between species might provide important insights into determining the cause of male-biased parasitism. Male biases in patterns of phoresy on hosts should only occur through morphological and ecological differences between the sexes. Reduced immunocompetence is not likely to play a role in generating a sex bias in phoresy because host fitness should not be significantly affected. Thus, if the immunocompetence theory is correct, fewer and weaker sex biases should be found in patterns of phoresy compared with patterns of parasitism. Lajeunesse et al. (2004) studied sex biases in patterns of parasitism by a water mite and phoresy by the mite's preinfective larvae on two dragonfly hosts. They found a male bias in both parasitic mites and preinfective phoretic larvae, which they concluded must have occurred because of ecological differences between the sexes. Here we investigated sex bias in the prevalence and infestation of a mite, *Thinoseius fucicola*, occurring phoretically on two species of seaweed fly hosts (Diptera: Coelopidae): *Coelopa frigida* and *Coelopa pilipes*.

Coelopa frigida is an established model organism for research into sexual selection and sexual conflict (Butlin et al. 1982; Gilburn and Day 1994, 1996, 1999; Day et al. 1996; Gilburn et al. 1996; Dunn et al. 2002; Blyth and Gilburn 2005, 2006; Edward and Gilburn 2007). The mating behavior of the other common British seaweed fly, *Coelopa pilipes*, has also been studied (Crean et al. 2000, Dunn et al. 2002, Edward and Gilburn 2007), albeit to a lesser extent. The two species occur on beaches on which deposits of seaweed, known as wrack beds, are washed up (Dobson 1974), often occurring sympatrically. The presence of a wrack bed can be unpredictable, with long periods of absence of seaweed at many sites (Day and Gilburn 1997). Seaweed flies live and breed throughout the year, responding not to seasons, but to the arrival of fresh deposits of seaweed whether these appear at the height of summer or middle of winter. *Thinoseus fucicola* parasitize talitrid ampihipods which also occur year-round within wrack beds. The mite occurs phoretically on both *C. frigida* and *C. pilipes*, using them as a means of transport between wrack beds. Both *C. frigida* and *C. pilipes* are sexually dimorphic, with males being more variable in size and possessing hairier legs in both species. Sexual selection favors large male size in both species (Gilburn et al. 1992, Crean et al. 2000) because large males are better at withstanding female resistance during premating struggles (Crean et al. 2000).

The purpose of this study is to investigate the extent that ecological differences between the sexes determine sex-biased phoresy in coelopids. The first aim of this study was determine whether a sex bias exists in the numbers of *T. fucicola* occurring on *C. frigida* and *C. pilipes*. The second aim was to determine whether the body size of coelopids, a sexually selected characteristic, is associated with phoretic mite load.

Materials and Methods

Experimental Procedures. We determined the prevalence and intensity of infestation (sensu Bush et al. 1997) of *T. fucicola* present on *C. frigida* and *C. pilipes* by collecting adult seaweed flies from several natural populations. Flies were collected using an aspirator in temperatures too cold for them to fly. Flies were collected from various sites in eastern Scotland in October 2004, namely Crail (Roome Bay, grid reference NO619079), St Monans (NO526014), and Elie (NT497996) in the East Neuk of Fife and Whitesands (NT709774) and Barns Ness (NT720773) in East Lothian. We also sampled flies from Boulmer (NU266141) in Northumberland, in northeast England in November 2004 and February 2005. Large numbers of *C. frigida* were only found at Crail; thus, *C. pilipes* alone was studied in the collections from the other sites. Flies were transported back to Stirling and their mite infestation level was determined under ×15 magnification. We also determined their wing length using a graticule unit under the same level of magnification. Wing length has been used as the standard index of relative size in numerous previous studies of coelopids (Gilburn et al. 1992; Gilburn and Day 1994, 1999; Dunn et al. 1999, 2002; Crean et al. 2000; Edward and Gilburn 2007; Meader and Gilburn 2008).

Analyses. We carried out all analyses using SPSS version 15.0. We generated binary logistic models of the prevalence of mites separately for each population. Sex of the fly was fitted to all models first, and size of the fly was added as a covariate; finally an interac-

Table 1. Prevalence (%) of *T. fucicola* on *C.frigida* at Crail and *C. pilipes* at five different UK sites for the two sexes separately

Species	Population	Females			Males		
		Prevalence	SE	*N*	Prevalence	SE	*N*
C. frigida	Crail	0.21	0.07	39	0.44	0.08	39
C. pilipes	Barns Ness	0.06	0.02	98	0.17	0.04	87
C. pilipes	Boulmer (Nov.)	0.11	0.04	73	0.28	0.06	50
C. pilipes	Boulmer (Feb.)	0.14	0.03	103	0.54	0.05	68
C. pilipes	Crail	0.06	0.02	188	0.20	0.03	184
C. pilipes	Elie	0.19	0.04	85	0.33	0.05	78
C. pilipes	St. Monans	0.16	0.03	186	0.20	0.04	107
C. pilipes	Whitesands	0.06	0.02	90	0.16	0.04	75

The site at Boulmer was sampled twice once in November and once in February.

Table 3. No. (infestation) of *T. fucicola* on *C.frigida* at Crail and *C. pilipes* at five different UK sites for the two sexes separately

Species	Population	Females			Males		
		Infestation	SE	*N*	Infestation	SE	*N*
C. frigida	Crail	5.50	1.90	8	8.53	2.40	17
C. pilipes	Barns Ness	1.67	0.42	6	1.60	0.21	15
C. pilipes	Boulmer (Nov.)	1.63	0.26	8	2.86	0.86	14
C. pilipes	Boulmer (Feb.)	1.29	0.16	14	1.62	0.15	37
C. pilipes	Crail	2.08	0.36	12	5.11	0.94	36
C. pilipes	Elie	1.81	0.38	16	2.08	0.32	26
C. pilipes	St. Monans	1.55	0.20	29	1.62	0.21	21
C. pilipes	Whitesands	1.00	0.00	5	1.33	0.14	12

The site at Boulmer was sampled twice in November and once in February.

tion term between sex and size was added. Wilcoxon median tests were used to compare the mean level of infestation between the sexes because the data were not normally distributed. Spearman's rank correlation coefficients were used to determine whether infestation level was related to size.

Results

Sex-Biased Prevalence of Mites. In *C. frigida* at Crail, significantly more males were found to possess mites than females (see Table 1 for summary data and Table 2 for analyses). A similar pattern was found in *C. pilipes* (Table 1) with a significant male bias in the presence of mites in six of the six populations sampled (Table 2).

Sex-Biased Intensity of Infestation of Mites. In *C. frigida*, infested males were not found to possess significantly (Wilcoxon $Z = -0.18$, $P = 0.86$) more mites than females (Table 3). Infestation levels (Table 3) were also not significantly different between the sexes in any population of *C. pilipes* (Barns Ness, Wilcoxon $Z = -0.09$, $P = 0.93$; Boulmer November collection, Wilcoxon $Z = -0.55$, $P = 0.58$; Boulmer February collection, Wilcoxon $Z = -0.58$, $P = 0.56$; Crail, Wilcoxon $Z = -1.78$, $P = 0.075$; Elie, Wilcoxon $Z = -1.21$, $P = 0.23$; St Monans, Wilcoxon $Z = -0.63$, $P = 0.53$; Whitesands, Wilcoxon $Z = -1.43$, $P = 0.15$).

Table 2. Logistic regression models of the prevalence of *T. fucicola* mites on coelopids collected from the east coast of Scotland and England

Species	Population	Sex		Size		Sex × size	
		χ^2	*P*	χ^2	*P*	χ^2	*P*
C. frigida	Crail	4.85	0.028	22.08	<0.001	1.08	0.30
C. pilipes	Barns Ness	5.776	0.016	10.420	0.001	6.83	0.009
C. pilipes	Boulmer (Nov.)	5.776	0.016	4.880	0.027	0.02	0.888
C. pilipes	Boulmer (Feb.)	32.783	<0.001	2.814	0.093	6.345	0.012
C. pilipes	Crail	14.938	<0.001	43.220	<0.001	1.03	0.309
C. pilipes	Elie	4.500	0.034	3.241	0.072	0.996	0.318
C. pilipes	St. Monans	0.770	0.380	2.753	0.097	0.008	0.929
C. pilipes	Whitesands	4.887	0.027	0.225	0.635	2.617	0.106

Models are fitted in a stepwise manner and df = 1 throughout all analysis.

Size-Biased Prevalence of Mites. Size was positively associated with the presence of mites in *C. frigida* (Table 2). Three populations of *C. pilipes* with male-biased prevalence also showed positive size-biased prevalence (Table 2). There was a significant sex–size interaction in the Barns Ness population and the February collection from Boulmer (Table 2). At Barns Ness, size was only positively associated with prevalence in males, whereas at Boulmer, mite prevalence only increased with size in females (Table 4).

Size-Biased Infestation of Mites. When considering only infested individuals, size was not associated with the level of mite infestation in *C. frigida* (Spearmans $\rho = -0.04$, $P = 0.86$) or four collections of *C. pilipes* (Barns Ness, $\rho = -0.05$, $P = 0.82$; Boulmer February collection, $\rho = +0.18$, $P = 0.22$; Elie, $\rho = +0.16$, $P = 0.30$; St Monans, $\rho = +0.23$, $P = 0.11$). However, size and level of infestation were positively correlated in the other three collections of *C. pilipes* (Boulmer November collection, $\rho = +0.63$, $P = 0.002$; Crail, $\rho = +0.44$, $P = 0.002$; Whitesands, $\rho = +0.61$, $P = 0.009$).

Relative Prevalence and Infestation in *C. frigida* and *C. pilipes*. A model of mite prevalence in the Crail collection that contained both species of coelopid showed an overall positive association between size and prevalence ($\chi^2_1 = 78.52$, $P < 0.001$), an overall male bias ($\chi^2_1 = 5.62$, $P = 0.018$), and a higher prevalence on *C. frigida* ($\chi^2_1 = 15.13$, $P < 0.001$). Adult *C.*

Table 4. Logistic regression models of the prevalence of *T. fucicola* mites on body size for each sex

Species	Population	Females			Males		
		χ^2	*P*	β	χ^2	*P*	β
C. frigida	Crail	11.19	0.001	0.29	11.96	0.001	0.17
C. pilipes	Barns Ness	0.63	0.43	−0.07	16.63	<0.001	0.21
C. pilipes	Boulmer (Nov.)	1.34	0.25	0.09	3.56	0.059	0.10
C. pilipes	Boulmer (Feb.)	14.97	<0.001	0.20	0.00	0.99	0.00
C. pilipes	Crail	5.66	0.017	0.11	38.60	<0.001	0.17
C. pilipes	Elie	0.02	0.90	0.01	4.22	0.04	0.08
C. pilipes	St. Monans	1.15	0.29	0.04	1.62	0.20	0.04
C. pilipes	Whitesands	1.33	0.25	−0.09	1.51	0.22	0.06

The β values are the logistic regression coefficients.

frigida were ~2.5 times more likely to possess mites ($\chi^2_1 = 15.05$, $P < 0.001$) than adult *C. pilipes.* There were no significant interaction terms. Among infected individuals, levels of infestation were not significantly different between the two species (Wilcoxon $Z = 0$, $P > 0.99$).

Discussion

Male-biased parasitism is generally believed to be associated with reduced immunocompetence in males as a result of testosterone (Folstad et al. 1989, Poulin 1996, Zuk and McKean 1996, McCurdy et al. 1998, Moore and Wilson 2002). The alternative explanation for male-biased parasitism is that ecological differences between the sexes results in different levels of infection. For example, differences in habitat, range, or behavior could result in different levels of exposure to parasites. However, a number of authors have criticized some studies reporting sex-biased parasitism because they have not attempted to identify any underlying ecological cause or adopted an inappropriate design to test between the two alternative hypotheses (Zuk and McKean 1996, Reimchem and Nosil 2001). Lajeunesse et al. (2004) suggested that studies of phoretic parasites might advance the study of the cause of male-biased parasitism because any biases found must have occurred through ecological or morphological differences between the sexes rather than variation in immunocompetence. Here we show a male bias in the proportion of individuals infected by the mite, *T. fucicola,* occurring phoretically on two species of seaweed fly hosts, *C. frigida* and *C. pilipes.* These are the first reported cases of a sex bias in phoresy on a host on which the parasite is solely phoretic. We conclude that this is likely caused by ecological differences between the sexes.

Two factors probably play a role in generating the male bias in the presence of mites. First, males are likely to be more active within wrack beds and moving between wrack beds in the search for females, thus increasing their exposure to mites. Furthermore, the greater movement of males is also likely to be more beneficial to the mites, generating a potential preference for being transported by a male because they are likely to move further and more often. A recent study of bat ectoparasites (*Spinturnix* spp.) showed that they have the ability to actively select the sex of their host (Christe et al. 2007). Perhaps *T. fucicola* might also possess a similar ability. Furthermore, males of both species have hairier legs than the females. The larger, thicker hairs of males might allow mites to attach themselves more easily, increasing the chances of infection. However, leg hairs cannot fully explain the patterns of phoresy seen because male *C. pilipes* have hairier legs than male *C. frigida,* yet *C. frigida* males had a higher level of mite prevalence in the population in which both species were occurring sympatrically. Indeed the higher levels of phoresy on male *C. frigida* adds further support to the idea that differences in mate searching explain the patterns of phoresy seen as male *C. frigida* show much higher rates of harassment of females than male *C. pilipes.* Thus, their increased level of movement and higher numbers of sexual encounters will increase their chances of becoming infected. It is also possible that the higher movement rate of males reduces the time that they might invest in grooming resulting in a higher mite load.

Moore and Wilson (2002) found that level of sexual size dimporphism and parasite infestation is related in mammals and suggested that this results from testosterone suppressing the immune system. However, a similar effect was not found in birds (McCurdy et al. 1998), although it might be present in grouse (Isomursu et al. 2006). Here we find that a strong male bias in phoresy of a mite occurring in some populations of two species of invertebrate with a male-biased sexual size dimorphism. Furthermore, larger males also had higher loads of phoretic mites in some populations. This is the first reported case of a size bias in phoresy. Large male size is sexually selected in both species; this suggests that correlations between sexual size dimorphism and levels of parasite infestation might also be generated through ecological differences. Our data support the claim of Reimchen and Nosil (2001) that ecological differences might play a more important role in generating male-biased parasitism than previously thought.

Zuk and McKean (1996) criticized many authors whose conclusions favored either a physiological or an ecological explanation for sex-biased parasitism because appropriate experiments were not carried out to distinguish between the two alternative hypotheses. One advantage of studying phoresy is that phoretic organisms are likely to have little effect on the fitness of their host. Thus, physiological causes of sex biases in prevalence and infestation can be ruled out. Thus, any bias found is likely to be ecological in nature. This study, like the previous one on dragonflies (Lajeunesse et al. 2004), found a male bias in phoresy. It should be noted that, in the dragonfly study, phoresy only occurred during preinfective larval stages of the mite before the mites become parasitic on the same host species, whereas in our study, adult mites were phoretic, using flies as a means of transport to their amphipod hosts. Despite the differences between these studies, both showed evidence of a sex bias in phoresy, which opens the possibility that a general male bias might possibly occur in patterns of phoresy, and the origin of this pattern is ecological in nature. Additional studies of patterns of phoresy on both vertebrate and invertebrate hosts would prove invaluable for determining whether there is a general male bias in patterns of phoresy. Furthermore, larger numbers of studies of patterns of phoresy would allow a comparison of the pattern of male bias seen in parasitism and provide an alternative mechanism of understanding the nature of sex biases in parasitism.

Acknowledgments

We thank M. Tinsley and two anonymous referees for helpful comments on an earlier draft of the manuscript.

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Received 16 April 2009; accepted 5 August 2009.